

LARVAL DEVELOPMENT OF TWO WESTERN AUSTRALIAN
SHRIMPS, *PALAEMONETES AUSTRALIS* DAKIN AND *PALAEMONETES*
ATRINUBES BRAY (DECAPODA, PALAEMONIDAE), REARED IN
THE LABORATORY.

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ABSTRACT

Larvae of the freshwater-estuarine species *Palaemonetes australis* pass through 3 zoeal stages without feeding and closely resemble those of the freshwater species *Macrobrachium australiense*. Larvae of the marine-estuarine species *Palaemonetes atrinubes* pass through 7 zoeal stages which require food and resemble those of the marine-estuarine species *Macrobrachium intermedium*. The number of zoeal stages, the development of pereopods and pleopods, and the morphology of the fifth abdominal somite appear to be related to habitat in these species and in North American species of *Palaemonetes*.

INTRODUCTION

Although larval development has been described for numerous species of Palaemoninae there have been few recent attempts to review differences in development between species and genera within this subfamily. Dobkin (1971) compared the number of larval stages in 6 North American species of *Palaemonetes* and found abbreviated development in the freshwater species (*P. paludosus* and *P. cummingi* but not in *P. kadiakensis* which was also from freshwater habitats). Williamson (1972) found that larval development in the African freshwater species *Macrobrachium niloticum* was not abbreviated when compared with development in *Macrobrachium intermedium* from marine habitats in east Australia.

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In this paper descriptions of larval development in 2 Western Australian species, *Palaemonetes australis* from freshwater and estuarine habitats and *Palaemonetes atrinubes* from marine and estuarine habitats, provide an opportunity for comparisons between: 1. larvae of species of *Palaemonetes* from different habitats in Australia, 2. larvae of species of *Palaemonetes* from Australia and North America, and 3. larvae of *Palaemonetes* and *Macrobrachium* from similar habitats in Australia.

MATERIALS AND METHODS

General

Ovigerous females of *Palaemonetes australis* were collected from freshwater habitats (salinity about $0.7^{\circ}/\text{‰}$) in the Canning River at the Kent St Weir and from estuarine habitats (salinity $25\text{--}35^{\circ}/\text{‰}$) in the lower Swan River at Nedlands Baths and held in water from the collecting sites. Larvae hatched from these females were maintained in compartments of polyethylene ice-cube trays. The trays were floated in water from the collecting site and the walls of each compartment were perforated to allow free exchange of water. Specimens of each larval stage were killed in 1% KOH, washed in tap water, fixed in 5% formalin and mounted in glycerol. Camera lucida drawings were prepared from larvae and exuvia of the Canning River series.

Ovigerous females of *Palaemonetes atrinubes* were collected from the lower Swan River at Point Walter in salinities of $25\text{--}35^{\circ}/\text{‰}$. Larvae hatched from these females were maintained as for *P. australis*. Specimens of each stage were prepared and drawn by the same method as for *P. australis*.

Feeding

In preliminary studies larvae of *P. australis* completed development to the megalopa stage without feeding and did not feed when supplied with particles of commercial fish food or *Artemia* nauplii.

Larvae of *P. atrinubes* died in the first or second larval stage unless fed. These larvae fed on particles of commercial fish food or *Artemia* nauplii. Survival was greatest when *Artemia* nauplii were supplied and they were used in the present study.

Terminology

The terminology suggested by Williamson (1969) is adopted here. A larva with natatory exopods on thoracic appendages and rudimentary pleopods is classed as a zoea with the stage given in roman numerals. A larva with setose natatory pleopods is termed a megalopa.

RESULTS

Palaemonetes australis

Egg Size

The size of eggs on specimens preserved in formalin varies with the stage of development. In the early stage of development, before eye spots are visible, eggs measure 1.0 by 1.4 mm and eggs with fully developed embryos measure 1.3 by 1.8 mm.

Incubation period

The duration of egg development varied with temperature and ranged from 73 days at 15°C (2 shrimp) to 19 days at 28°C (3 shrimp).

Number of larval stages

Of 50 larvae hatched from eggs at each of the salinities, 1‰ and 35‰, all reached the megalopa stage after passing through 3 clearly recognised zoeal stages with a single moult at each stage.

Duration of larval development

Time from hatch to the megalopa stage varied with temperature and ranged from 4.5 days at 28°C (10 larvae) to 17 days at 15°C (10 larvae). The zoeal stages were of about equal duration.

Size of stages

The overall length for 21 stage I larvae ranged from 4.4 to 5.6 mm and averaged 5.0 mm. No growth was apparent in other stages and 30 megalopa stage shrimp ranged in length from 4.5 to 5.8 mm and averaged 5.2 mm.

Development of larvae

Carapace (figures 3–6) with rostrum shorter than antennular peduncle in all stages; without dorsal spines in stage I, with single dorsal spine in stages II and III and 3 dorsal spines in megalopa; with single epigastric tubercle in stage III; with supra-orbital spines in stages II and III; with branchiostegal groove in megalopa; with single pair of small spines on antero-ventral margins in stage I and 2 pairs of such spines in stages II, III and megalopa.

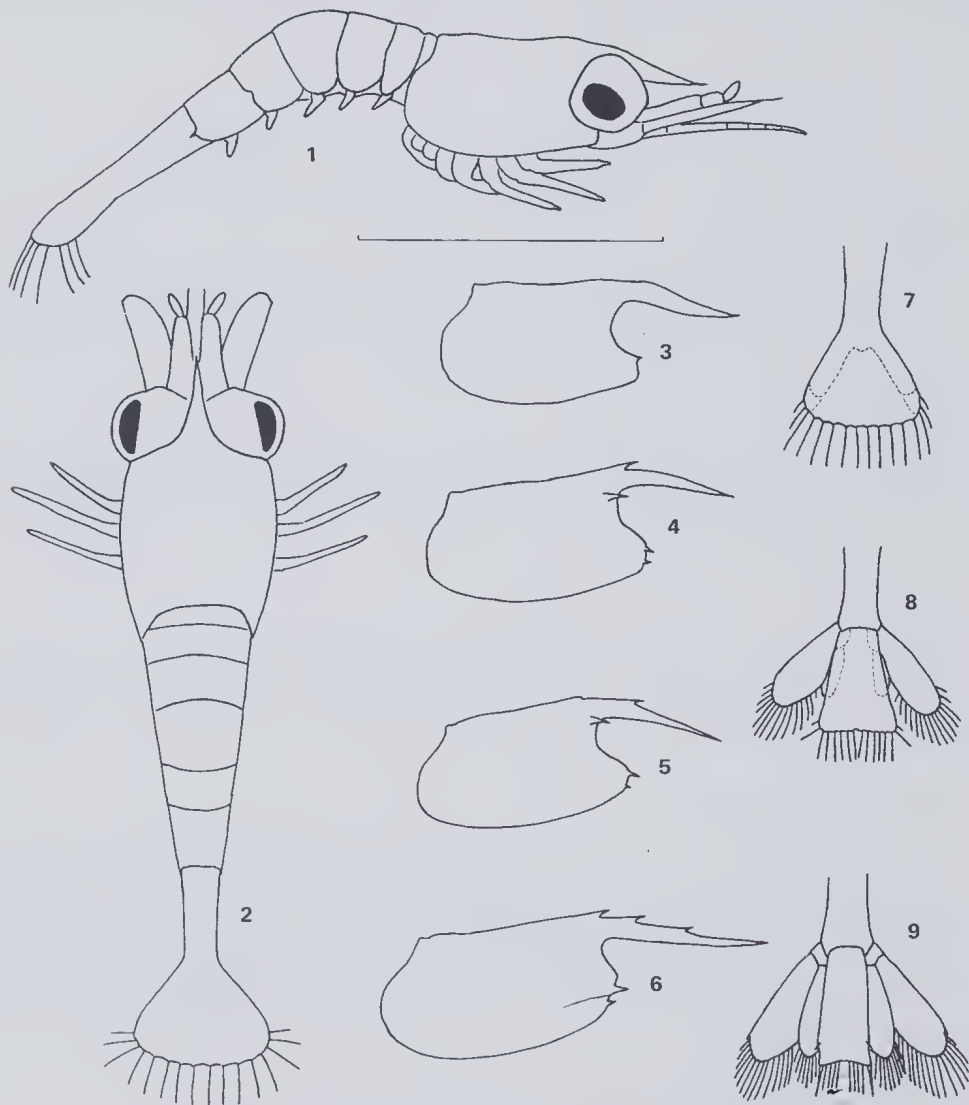
Abdomen (figures 26-29) with posterior margin of fifth somite pointed in stages I and II and bluntly angled in stage III and megalopa.

Telson (figures 2,7-9) triangular, posterior margin convex with 8+8 processes in stages I and II; articulated with sixth somite, elongated in shape, posterior margin straight with 8+8 processes in stage III; rectangular,

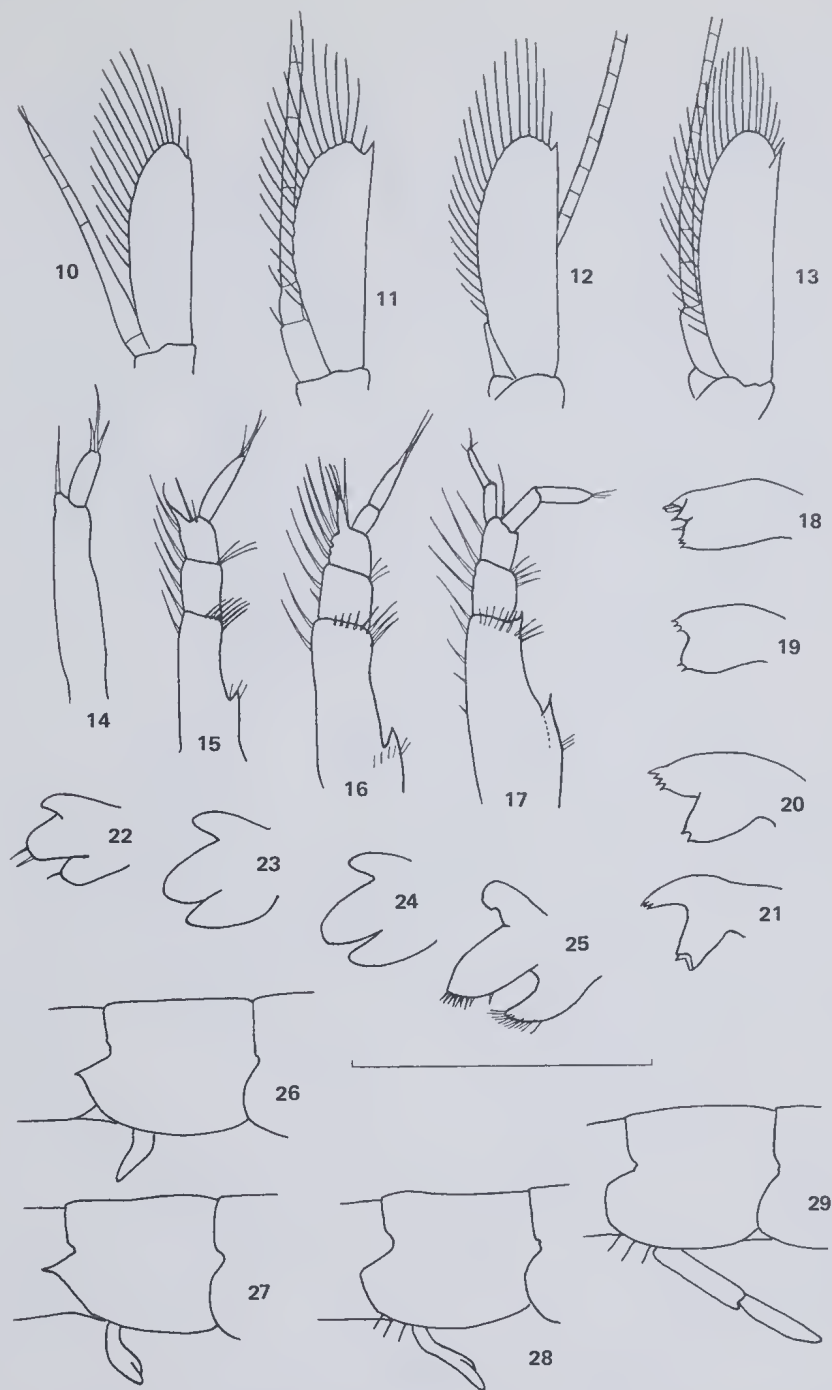
posterior margin concave with 5+5 processes, lateral margins with single pair of small processes in megalopa.

Uropods (figures 8–9) present in stage III and megalopa, with small spine on postero-lateral margin of exopod in megalopa.

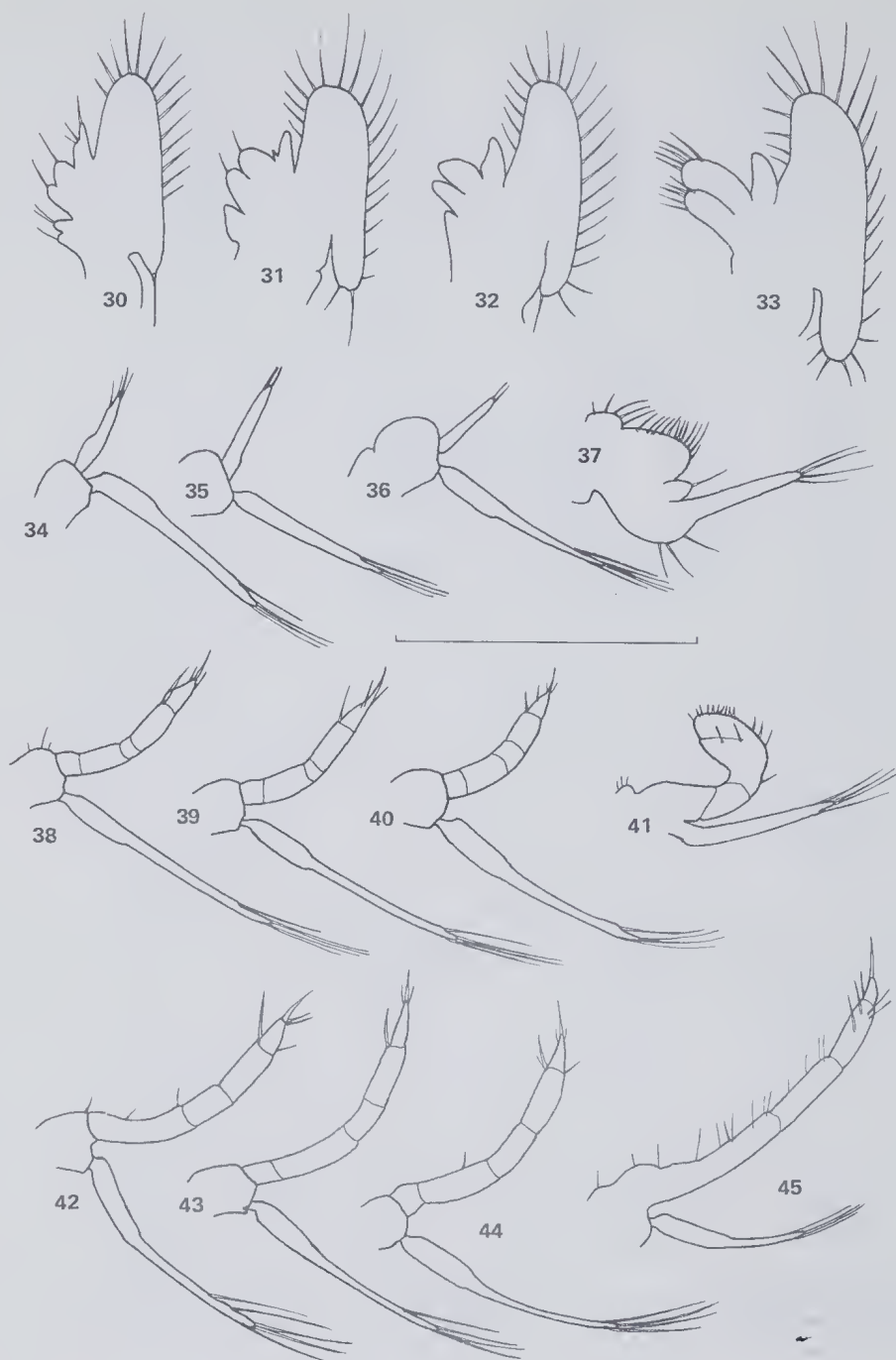
Antennular penduncles (figures 14–17) straight, unsegmented in stage I; of 3 segments with stylocerite on outer margin of basal segment in



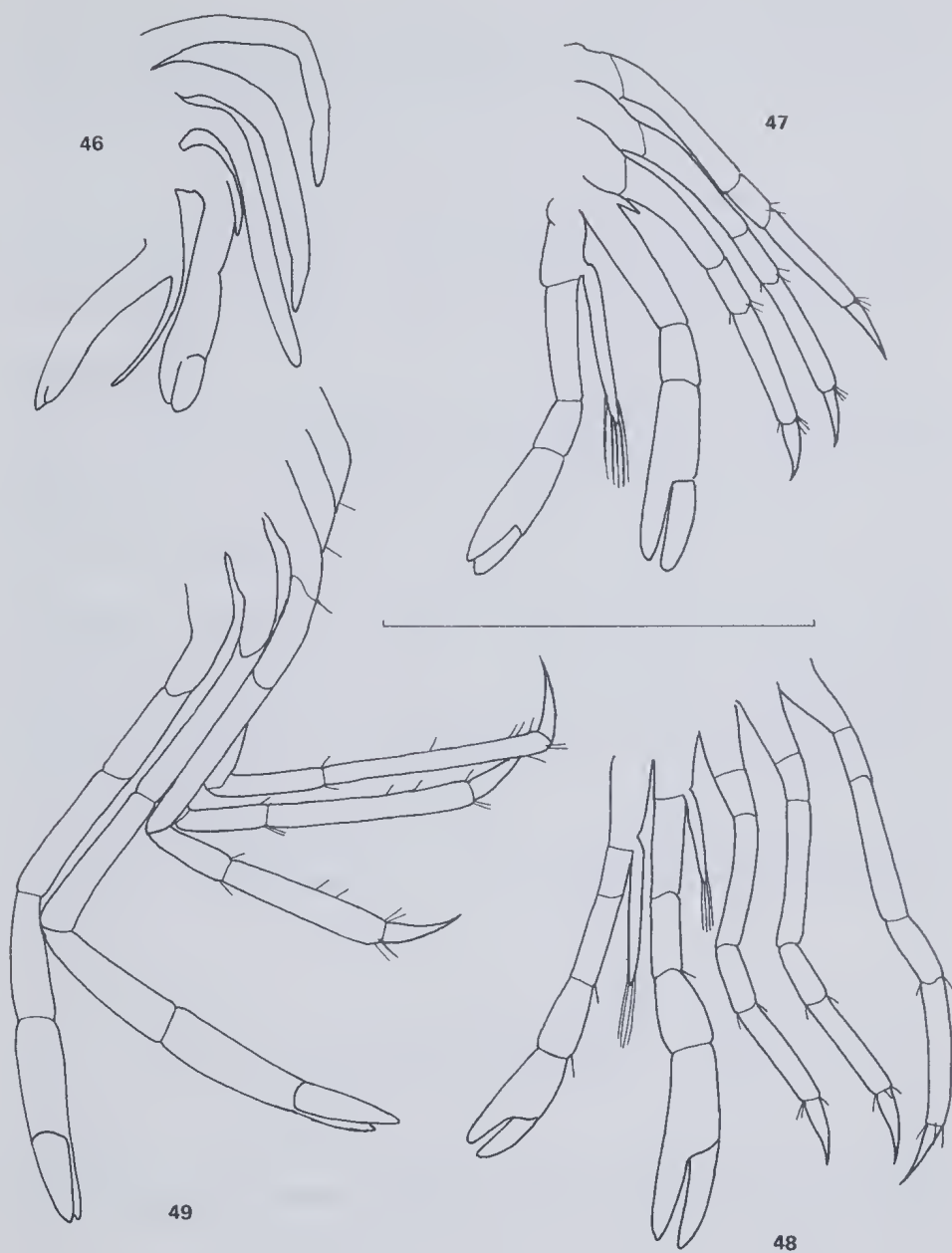
Figures 1-9, *Palaemonetes australis*. 1, 2 zoeal stage I; 3-6 carapace, zoeal stages I-III, M (megalopa); 7-9, telson, zoeal stages II-III, megalopa. Scale line represents 2 mm. Setae omitted from appendages in 1-6.



Figures 10-29, *P. australis*. 10-13, antenna I-III, M; 14-17, antennule I-III, M; 18-21, mandible I-III, M; 22-25, maxillule I-III, M; 26-29, fifth abdominal somite I-III, M. Scale line represents: 10-13, 1 mm; 14-17, 26-29, 0.8 mm; 18-21, 0.4 mm; 22-25, 0.5 mm.



Figures 30-45, *P. australis*. 30-33, maxilla I-III, M; 34-37, first maxilliped I-III, M; 38-41, second maxilliped I-III, M; 42-45, third maxilliped I-III, M. Scale line represents: 30-33, 0.5 mm; 34-45, 0.7 mm.



Figures 46-49, *P. australis*, pereiopods I-VI, stages I-III, M. Scale line represents 1 mm.

stages II+; outer ramus of antennule segmented in stages III+ and inner ramus segmented in megalopa.

Antenna (figures 10–13) with endopod segmented and longer than exopod in all stages; exopod (scale) unsegmented with straight outer margin in all stages and antero-lateral spine in stages II+.

Mandible (figures 18–21) with molar and incisor processes in all stages and with 2 spines between these processes in stage I.

Maxillule (figures 22–25) trifid; with endopod unsegmented, bearing a single seta in stage I and numerous setae in megalopa; centre lobe with numerous short setae in megalopa.

Maxilla (figures 30–33) with 3 inner lobes; exopod with narrow lobe terminating in single seta in stage I and 2–4 setae in stages II+.

First maxilliped (figures 34–37) with endopod small and unsegmented in all stages; exopod with 4–6 setae in stages I–III and short with 4 setae in megalopa; inner lobe with numerous setae in megalopa.

Second maxilliped (figures 38–41) with endopod segmented and fifth segment terminating in a stout spine in stages I–III, hook shaped with numerous short setae on terminal segment in megalopa; exopod longer than endopod in stages I–III, shortened in megalopa.

Third maxilliped (figures 42–45) with endopod segmented, terminating in stout spine in all stages; exopod as long as endopod in stages I–III, without exopods in megalopa.

Third, fourth and fifth pereopods (figures 46–49) without exopods in all stages, unsegmented in stage I, segmented with stout terminal spine in stages II+.

Pleopods (figures 1,26–29) present as uniramous buds in stage I, biramous in stages II–III, segmented with setae in megalopa.

Palaemonetes atrinubes

Egg Size

Eggs on specimens preserved in formalin measured 0.6 by 0.8 mm in early stages of development and 0.7 by 0.9 mm when mature.

Incubation period

At 25°C the incubation period was 11 days for a single female which laid eggs in the laboratory.

Number of stages

In 30 larvae hatched from eggs the first 6 moults corresponded to well defined zoeal stages. Morphology was little changed in subsequent moults and 5 larvae reached the megalopa stage after 7–10 moults. For this description 7 zoeal stages and 1 megalopa are recognised.

Duration of larval development

The time from hatch to megalopa stage varied with temperature and ranged from 20–24 days at 29°C (3 larvae) to 40–44 days at 19°C (2 larvae). Larvae moulted regularly to reach stage V at about $\frac{1}{3}$ of the total development time and subsequent moults were less frequent.

Size of stages

First stage zoeae were 2.9–3.1 mm overall length (10 larvae), stage III zoeae were 4.0–4.5 mm (10 larvae) and stage VII zoeae were 7.0–8.1 mm (6 larvae).

Development of larvae

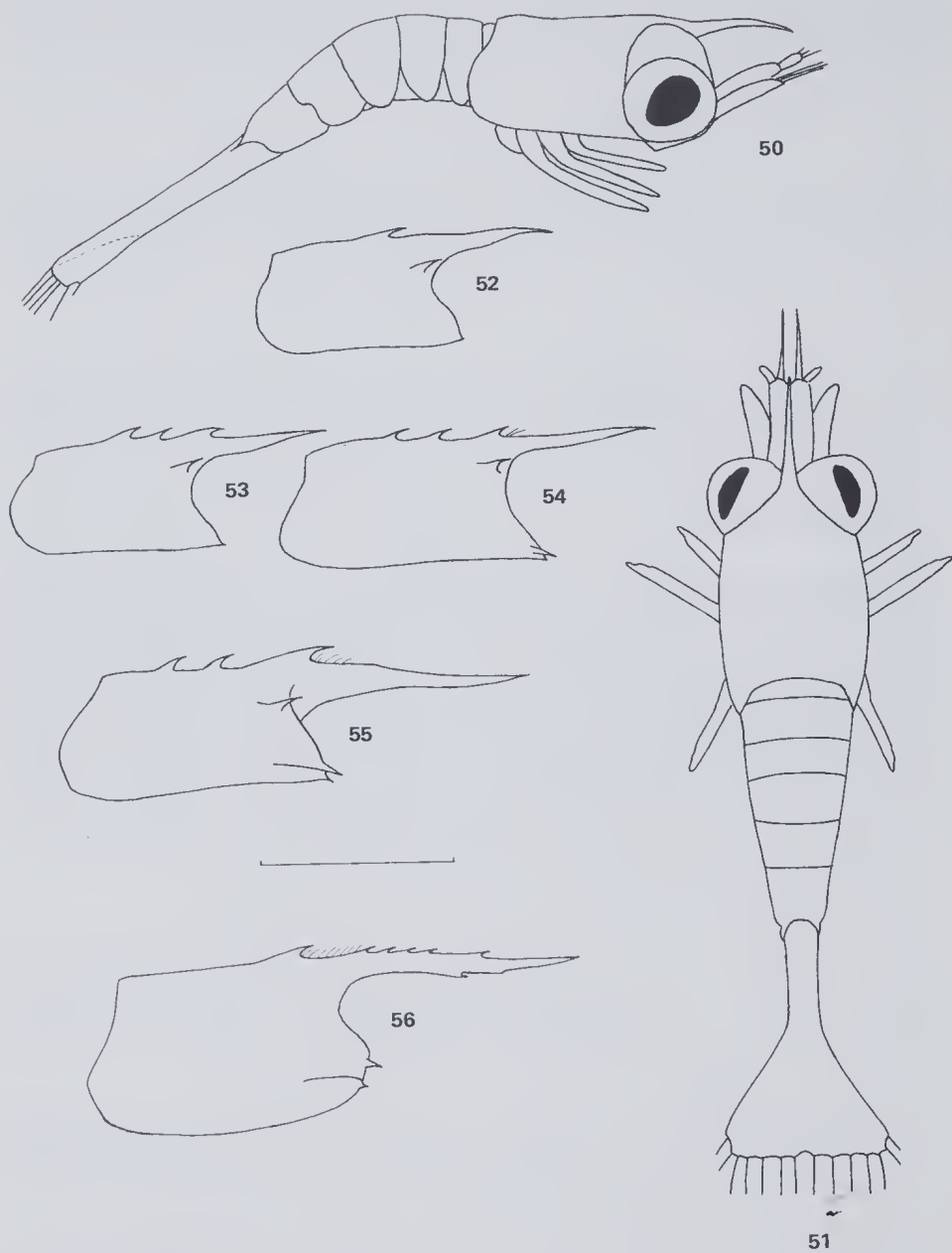
Carapace (figures 50–56) with rostrum about as long as antennular peduncle, unarmed in all zoeal stages and with rostral formula 5/2 in megalopa; with single epigastric spine in stage II, 3 epigastric spines in stages III+; supra-orbital spines in zoeal stages II+; pterygostomian spine small in stage I, progressively elongated in stages II–V, raised above ventral margin with a new smaller spine in pterygostomian position in stages V–VII; antennal and branchiostegal spines on anterior margin of carapace in megalopa; branchiostegal groove present in megalopa.

Abdomen (figures 50, 57–59) with strong spine on posterior margin of fifth somite in all zoeal stages and small spine in megalopa.

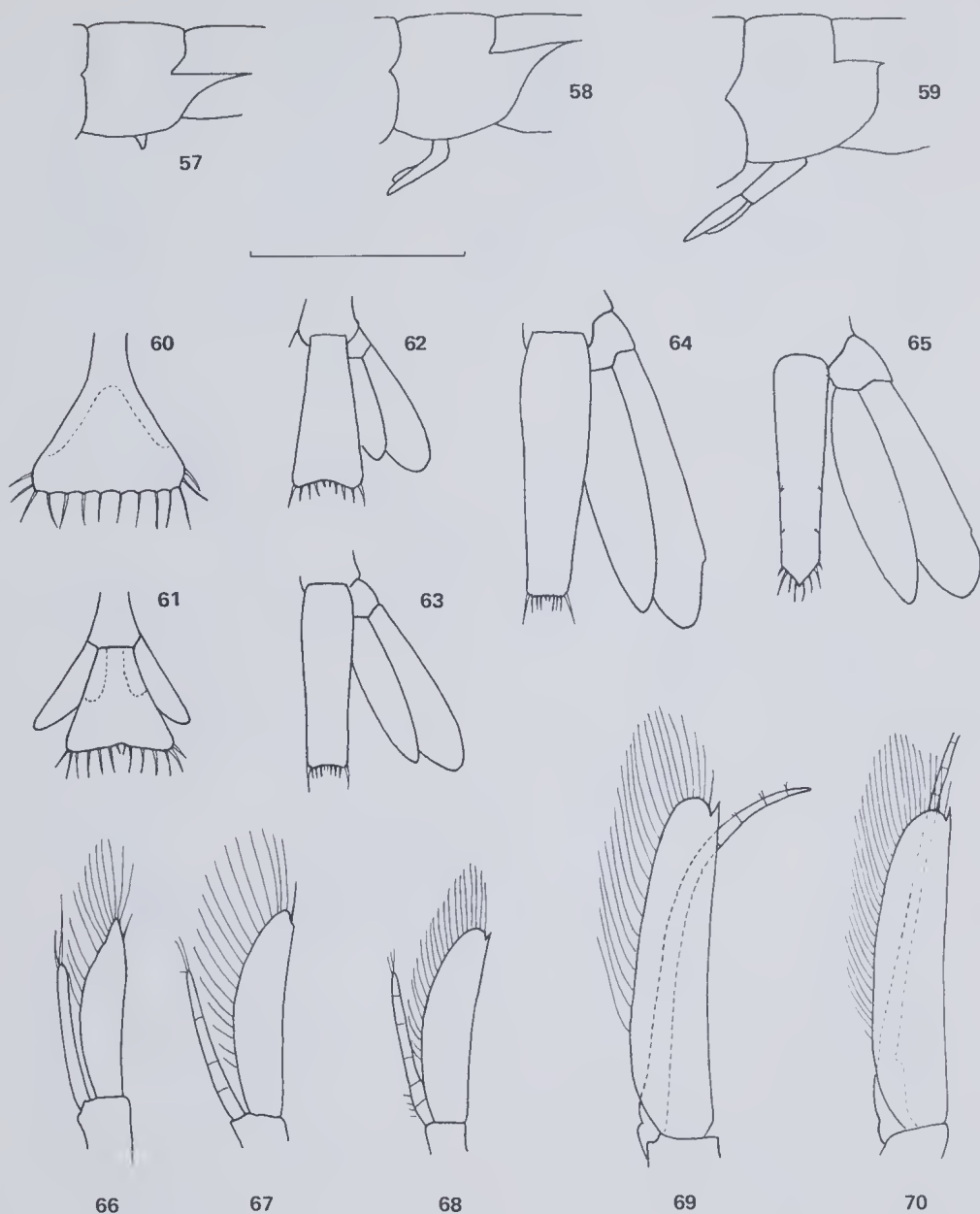
Telson (figures 51, 60–65) triangular in stages I–III, elongated rectangular in all other stages; with posterior margin straight with 7+7 processes in stages I–II, concave with 7+7 processes in stage III, concave with 5+5 processes in stages IV–VII, pointed with 4+4 processes in megalopa; with 2 pairs of dorsal setae near lateral margins in megalopa.

Uropods (figures 61–65) present in stages III+, segmented in stages IV+; with indentation on postero-lateral margin of exopod in stage VII, postero-lateral spine on exopod in megalopa.

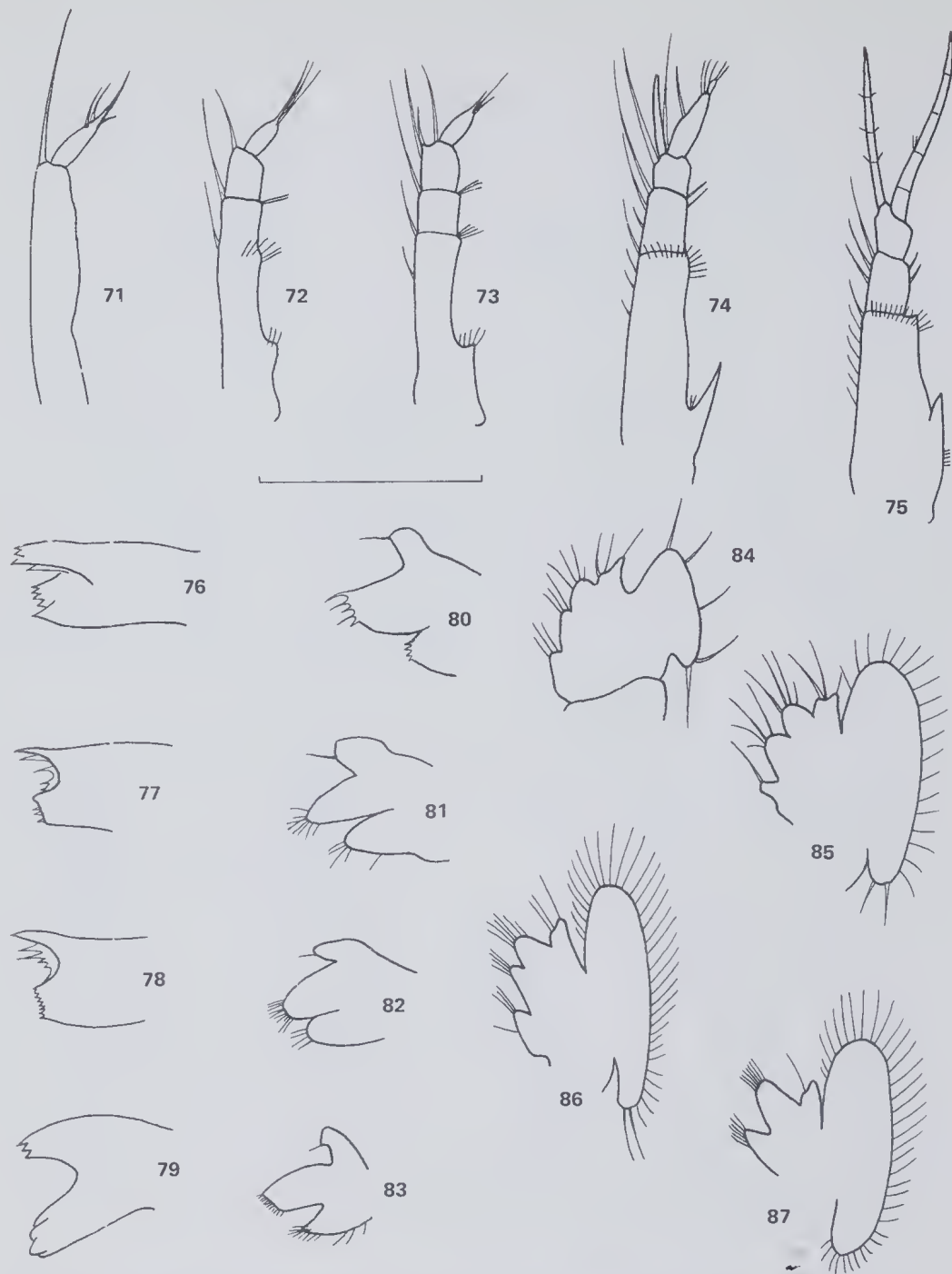
Antennular peduncle (figures 71–75) unsegmented in stage I, with 2 segments in stage II and 3 segments in stages III+; stylocerite as a lateral lobe on basal segment in stages II–III, pointed in stages IV+; inner ramus unsegmented in all zoeal stages, segmented in megalopa; outer ramus unseg-



Figures 50-56, *P. atrinubes*. 50-51 zoeal stage I; 52-56 carapace, stages II, III, V, VII, M. Scale represents 1 mm.



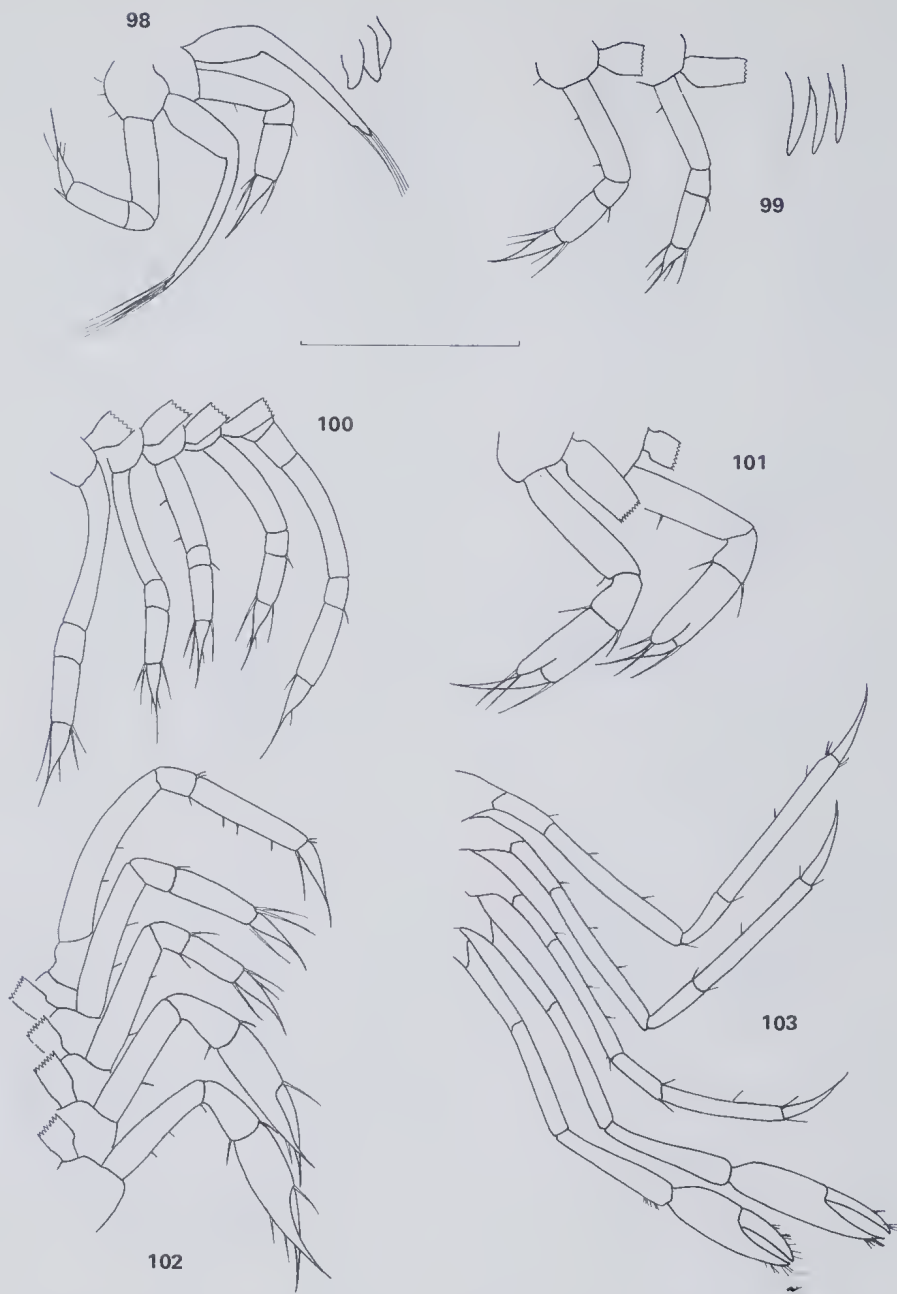
Figures 57-70, *P. atrinubes*. 57-59, fifth abdominal somite, stages IV, VII, M; 60-65 telson, stages II, III, IV, VI, VII, M; 66-70 antenna, stages II, III, V, VII, M. Scale represents: 57-59, 66-67, 0.6 mm; 60-65, 68-70, 0.8 mm.



Figures 71-87. *P. atrinubes*. 71-75 antennule, stages I, II, III, VII, M; 76-79 mandible, stages I, VI, VII, M; 80-83 maxillule, stages I, VI, VII, M; 84-87 maxilla, stages I, VI, VII, M. Scale line represents: 71-75, 0.5 mm; 76-79, 0.25 mm; 80-87, 0.35 mm.



Figures 88-97, *P. atrinubes*. 88-91 first maxilliped, I, III, VII, M; 92-94 second maxilliped, I, VII, M; 95-97 third maxilliped, I, VII, M; exopods partly omitted in 93, 96. Scale line represents: 0.5 mm.



Figures 98-103, *P. atrinubes*, pereopods I - V, stages II, III, IV, VI, VII, M. Exopods partly omitted 99-102. Legs III-V omitted, 101. Scale line represents: 98-100, 0.5 mm; 101-103, 0.7 mm.

mented in stages I–VI, with 2 segments in stage VII and 5 segments in megalopa.

Antenna (figures 66–70) with endopod shorter than exopod and unsegmented in stages I–II, as long as exopod and segmented in stages III–V, longer than exopod and segmented in stages VI+; exopod (scale) with 5 terminal segments in stage I, 4 segments in stage II, unsegmented in stages III+.

Mandible (figures 76–79) with 2 spines between molar and incisor processes in stage I, 3 such spines present in stages II–VII but not present in megalopa.

Maxillule (figures 80–83) trifold with exopod terminating in single seta, inner lobes with numerous terminal setae.

Maxilla (figures 84–87) with 4 inner lobes in all zoeal stages, 3 inner lobes in megalopa; exopod with 5 setae in stage I and numerous setae in later stages.

First maxilliped (figures 88–91) with endopod smaller than exopod, unsegmented; exopod with 4–6 terminal setae; inner lobes with numerous short setae in megalopa.

Second maxilliped (figures 92–94) with endopod segmented and terminal segment with stout spine in all zoeal stages, hook shaped with numerous setae on terminal segment in megalopa; exopod longer than endopod.

Third maxilliped (figures 95–97) with endopod segmented and terminating in stout spine; exopod slightly longer than endopod in zoeal stages, about half length of endopod in megalopa.

First and second pereopods (figures 98–103) present as bifid rudiments in stage I; with fully developed exopod in stages II–VII; endopod segmented with strong terminal spine in stages II–V, terminal segment bifid in stage VI and chelate in later stages.

Third, fourth and fifth pereopods (figures 98–103) absent in stage I; present as rudiments in stages II–III; with exopods on third and fourth pereopod, but not on fifth pereopod, in stages IV–VII; endopods segmented with strong terminal spines in stages IV+.

Pleopods (figures 57–59) present as buds in stage IV, bifid in stage VII and with setae in megalopa.

Discussion

Larval development is more rapid in the freshwater species *Palaeomonetes australis* than in the marine-estuarine species *Palaeomonetes atrinubes*. Larvae of *P. australis* did not feed and completed the 3 zoeal stages in 4–17 days while larvae of *P. atrinubes* required food and completed the 7 zoeal stages in 20–44 days. Pereopods and pleopods are present

in stage I larvae of *P. australis* while *P. atrinubes* larvae are without third, fourth and fifth pereopods until stage II and without pleopods until stage IV. Larvae of these species also differ in the postero-lateral margins of the fifth abdominal somite which bear strong spines in all zoeal stages of *P. atrinubes* while in *P. australis* short spines occur in stages I–II but not in stage III.

Comparison between larval development in Australian and North American species of *Palaemonetes*, using published descriptions, indicates that the differences between larvae of *P. australis* and *P. atrinubes* may be related to habitat. The American freshwater species *Palaemonetes paludosus* and *Palaemonetes cummingi* undergo abbreviated larval development (Dobkin, 1963, 1971) similar to that in *P. australis*. These larvae do not feed and the postero-lateral margin of the fifth abdominal somite is without spines. Larvae of the American species *Palaemonetes pugio* and *Palaemonetes vulgaris* from estuarine-marine habitats pass through 7–11 zoeal stages (Broad, 1957) which resemble those of *P. atrinubes*. All stages require food and postero-lateral spines are present on the fifth abdominal somite in all zoeal stages except stage I. Development in the American freshwater species *Palaemonetes kadiakensis* appears to be intermediate between the other groups, with 6 zoeal stages all of which require food and with pleopods absent from stages I–II (Broad and Hubschman, 1963). However, in common with the other freshwater species the postero-lateral margin of the fifth abdominal somite is without spines. Thus species of *Palaemonetes* from Australia and North America exhibit abbreviated larval development and reduction, or absence, or the postero-lateral spines of the fifth abdominal somite in freshwater habitats.

Similar adaptation of larval development to habitat is apparent in 2 Australian species of the genus *Macrobrachium*. In the freshwater species *Macrobrachium australiense* larvae develop, without feeding, through 3 zoeal stages all without postero-lateral spines on the fifth abdominal somite (Fielder, 1970). These larvae closely resemble corresponding stages in *P. australis*, *P. paludosus* and *P. cummingi*. Larvae of the marine-estuarine species *Macrobrachium intermedium* require food and pass through 10 zoeal stages with strong postero-lateral spines on the fifth abdominal somite in stages II–X (Williamson, 1972). Thus larval development in *M. intermedium* resembles that in *P. atrinubes*, *P. pugio* and *P. vulgaris*.

Although larval development in the Australian species *P. australis*, *P. atrinubes*, *M. intermedium* and *M. australiense* appears to be related to habitat specific differences occur and identification of larvae of these species can be facilitated by the use of the following key:

1. Three zoeal stages. Stage I with pereopods III–V and pleopods rudimentary. Stages II–III with pereopods III–V segmented, without

- strong postero-lateral spine on fifth abdominal somite. Freshwater or estuarine habitats 2
- Seven or more zoeal stages. Stage I without pereopods III-V or pleopods. Stages II+ with strong postero-lateral spine on fifth abdominal somite. Marine or estuarine habitats 3
2. Stage I zoeae with posterior margin of telson convex and bearing 8+8 processes. Stages II-III with single dorsal carapace spine *Palaemonetes australis*
- Stage I zoeae with posterior margin of telson straight and bearing 7+7 processes. Stages II-III without dorsal carapace spines *Macrobrachium australiense*
3. Stage I zoeae with postero-lateral spines on fifth abdominal somite. Stages II+ with 3 dorsal carapace spines *Palaemonetes atrinubes*
- Stage I zoeae without postero-lateral spines on fifth abdominal somite. Stage II with single dorsal carapace spine and stages III+ with 2 such spines *Macrobrachium intermedium*

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